



## Behavioural responses of sympatric rodents to complete pilferage

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Food-hoarding animals employ a variety of tactics to minimize the loss of caches to pilferers. It remains unclear, however, how these responses are affected by complete pilferage events and if differences occur between species and between the sexes within a species that adopt different hoarding strategies. We studied the behavioural responses to complete pilferage in five species that scatter-hoarded or larder-hoarded. Under natural conditions and within outdoor enclosures we simulated complete pilferage events by removing wild apricot, *Prunus armeniaca*, seeds hoarded by Pere David's rock squirrels, *Sciurotamias davidianus*, Korean field mice, *Apodemus peninsulae*, striped field mice, *Apodemus agrarius*, Chinese white-bellied rats, *Niviventer confucianus*, and rat-like hamsters, *Tscherskia triton*. Following pilferage, all five species increased seed removal from the source and total hoarding intensity under both natural and captive conditions, but no effect of sex was found. Pere David's rock squirrels, Korean field mice and striped field mice, which show both scatter and larder hoarding, increased scatter hoarding, but not larder hoarding. Our pilferage manipulations in the field also increased the distance that seeds were buried from the source. These findings suggest that complete pilferage may increase seed-hoarding behaviour in rodents and that scatter hoarding might be better than larder hoarding in avoiding complete pilferage in rodents that already perform both of these.

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Food hoarding is a strategy adopted by many species in response to temporal variation in the availability of resources (Vander Wall 1990; Tsurim & Abramsky 2004); however, hoarded food must be protected from pilfering competitors. Food pilferage is as common as food hoarding, and while this benefits the pilferer, cache loss reduces the hoarders' food storage and threatens their survival and reproductive capacity during periods of food scarcity (Wauters et al. 1995; Vander Wall & Jenkins 2003; Gerhardt 2005). Not surprisingly, food hoarders have evolved a series of strategies to deal with the risk of pilferage by competitors (reviewed by Vander Wall & Jenkins 2003; Dally et al. 2006).

According to the pilferage avoidance hypothesis, hoarders are able to adopt different tactics to minimize cache loss (Macdonald 1976; Vander Wall & Jenkins 2003; Dally et al. 2006). Birds and mammals known to hoard show a wide variety of avoidance strategies including modifying consumption and caching rates (Brotons 2000; Pravosudov & Lucas 2000; Emery et al. 2004),

recovering and moving caches repeatedly (Emery & Clayton 2001, 2004; Bugnyar & Kotrschal 2002; Emery et al. 2004), aggressively preventing access to cached items (Clarke & Kramer 1994), shifting from scatter hoarding to larder hoarding (Jenkins et al. 1995; Preston & Jacobs 2001), avoiding and delaying caching when in the presence of potential thieves (Burnell & Tomback 1985; Bugnyar & Kotrschal 2002), and spacing caches further apart or out of sight (Bugnyar & Kotrschal 2002; Dally et al. 2005; Gálvez et al. 2009). Common ravens, *Corvus corax*, rooks, *Corvus frugilegus*, and eastern grey squirrels, *Sciurus carolinensis*, also use misinformation (e.g. empty caches) to confuse potential robbers or conspecifics (Bugnyar & Kotrschal 2004; Dally et al. 2006; Steele et al. 2008).

In contrast to avoidance, the pilferage tolerance hypothesis posits that food hoarders cannot avoid or prevent pilferage and instead steal food items from other hoarders to compensate for their own losses (Vander Wall & Jenkins 2003). Under this model, pilferage is reciprocal and, as such, tolerated. Many long-term hoarding species that live in environments with high rates of cache loss may have evolved mechanisms for tolerating pilferage (Vander Wall & Jenkins 2003). For example, social animals such as jays (*Perisoreus* spp.), and solitary rodents with overlapping home ranges such as red squirrels, *Sciurus vulgaris*, field mice (*Apodemus* spp.) and agoutis (*Dasyprocta* spp.) appear to tolerate pilferage (Vander Wall & Jenkins 2003). However, this pilferage tolerance hypothesis lacks theoretical

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support and the application of game-theoretical models is not possible if animals are simply exchanging caches. For example, the best exchange that hoarders could achieve would be somewhat worse than if they simply protected their own caches. Furthermore, hoarders would do much worse if they relied only on others' caches because retrieval of these caches is generally less rewarding than protecting and retrieving their own caches.

These two models are not mutually exclusive (if they are both valid): pilferage avoidance strategies are used to minimize cache loss, and pilferage tolerance strategies are used to compensate for such loss. While this field of ecology has received much attention, little is known about how these models apply to situations involving the complete loss of an animal's food store. Only one study, on western scrub-jays, *Aphelocoma californica*, has examined how hoarders respond to unrewarded hoarding efforts and this showed that their hoarding behaviour did not cease when hoarding efforts were unrewarded and they had no choice of where to cache food (de Kort et al. 2007).

We aimed to investigate how hoarding behaviour in small rodents changes following complete cache loss. We conducted complete pilferage experiments using five sympatric rodent species residing within naturalistic enclosures and in the field. We chose Pere David's rock squirrels, *Sciurotamias davidianus*, Korean field mice, *Apodemus peninsulae*, striped field mice, *Apodemus agrarius*, Chinese white-bellied rats, *Niviventer confucianus*, and rat-like hamsters, *Tscherskia triton*, as our focal models. Pere David's rock squirrels, Korean field mice and striped field mice are known to scatter-hoard and larder-hoard food, and Chinese white-bellied rats and rat-like hamsters are known to larder-hoard only (Lu & Zhang 2008). The pilferage avoidance hypothesis predicts that when faced with complete cache loss, rodents should store seeds further away, and shift from larder hoarding to scatter hoarding to avoid cache loss. Under the same scenario, the pilferage tolerance hypothesis posits that rodents should disperse cached items at a greater rate to compensate for losses.

## METHODS

### Study Site and Subjects

Our study was conducted at the Liyuanling research station (40°00'N, 115°30'E; 1140 m above sea level) in the Donglingshan Mountains approximately 120 km northwest of Beijing city. This area has a temperate continental monsoon climate, a mean annual temperature of 10 °C and receives 600 mm of precipitation annually. The region is dominated by shrub land, secondary forest and abandoned farmland and has historically been disturbed by people and livestock. Dominant tree species include Liaodong oak, *Quercus liaotungensis*, wild walnut, *Juglans mandshurica*, wild apricot, *Prunus armeniaca*, wild peach, *Amygdalus davidiana*, and Chinese pine, *Pinus tabulaeformis*. Cultivated walnut, *Juglans regia*, is also heavily distributed throughout abandoned agricultural land. The five rodent species studied here are common throughout the study area (Li et al. 2004). This location has been the subject of much of

our previous work and further information can be obtained from Zhang et al. (2008, 2009).

We caught animals for use in the enclosure experiments from the study area, but not from areas where experiments were performed in the field (>500 m away from the field experimental plot). The number of each species and their hoarding characteristics are outlined in Table 1. We conducted trapping from June to September 2009 using steel-wire live traps (12 × 12 cm and 25 cm high). Fresh peanuts were used as bait, small pieces of cabbage were provided as a water supply and local dry leaves were provided as nest material. An iron sheet was attached on the upper side of the trap as shelter to protect from predation and sunshine (following Zhang & Zhang 2008; Zhang et al. 2008, 2009). We laid traps (20–30) every 5 m along five or six transect lines between 1800 and 1900 hours. Traps were then checked at sunrise (0600–0700 hours) and sunset (1800–1900 hours) over 3 days. Pregnant and lactating females were released immediately on site. Captured animals were carefully transferred to the laboratory using the live trap and housed individually in plastic boxes (37 × 26 cm and 17 cm high) in a room at 18–25 °C and a light-dark cycle of 14:10 h (lights on at 0530 hours). Commercial mouse chow (Keao Feed Ltd., Beijing, China), water and nest structures were provided ad libitum. Animals were acclimatized in the laboratory at least a week prior to testing. We recorded sex, mass, breeding status and age of each trapped animal. After our study, animals were retained in the laboratory and used for other studies. Animals maintained their health and weight during captivity. All field and laboratory protocols were approved by the Wuhan Municipal Science and Technology Commission and the Institute of Zoology, Chinese Academy of Sciences.

### Enclosure Experiments

These experiments were conducted from September to October (autumn) 2009 during which rodents were actively seed hoarding in preparation for winter. Twelve enclosures (4 × 3 m) were constructed in open fields around our research station using sheet iron with a thickness of 1 mm (following Lu & Zhang 2005). Each wall was placed at a depth of 30 cm underground and the height of each wall was 1 m above ground level. Each enclosure was covered with a 1 × 1 cm wire mesh that prevented focal animals escaping or other animals entering. Vegetation inside the enclosures was removed and the ground covered with 5–10 cm of sandy soil as the seed-hoarding substrate. A woody nest (20 × 30 cm and 20 cm high) and a water plate were placed in one corner of each enclosure. Seed stations (50 × 50 cm) were located at the centre of each enclosure.

Wild apricot is a common tree in secondary forest and shrub land throughout the study area (Lu & Zhang 2005). Wild apricot seeds (mean ± SD) weigh 1.2 ± 0.2 g, are 22.1 ± 1.6 mm long and 9.8 ± 0.8 mm wide (including endocarp, *N* = 50, data not shown). They ripen in the middle of July and because of their high nutritional content (53.1% crude fat, 25.5 J/g calorific value) are favoured food items that are both eaten and hoarded by the five rodent species used here (Zhang & Zhang 2008).

**Table 1**  
Species and subjects involved in a complete pilferage experiment conducted within outdoor enclosures

Species	Samples	Body length (mm)	Body weight (g)	Seed-hoarding pattern	Habit
<i>Sciurotamias davidianus</i>	8♂8♀	210.2±7.3	222.1±23.7	Scatter & Larder	Diurnal
<i>Apodemus peninsulae</i>	6♂6♀	92.0±6.2	23.5±4.1	Scatter & Larder	Nocturnal
<i>Apodemus agrarius</i>	5♂7♀	102.7±10.0	29.2±7.2	Scatter & Larder	Nocturnal
<i>Niviventer confucianus</i>	7♂5♀	128.1±11.3	62.7±10.1	Larder	Nocturnal
<i>Tscherskia triton</i>	6♂6♀	132±11.4	120.3±8.6	Larder	Nocturnal

Values are mean ± SD.

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